BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. September 18, 1958 Number 94

AFFINITIES OF THE PATAGONIAN FOSSIL MAMMAL NECROLESTES

By Bryan Patterson

Since its description by Ameghino in 1891, the curious little fossorial *Necrolestes* from the Santa Cruz beds has never rested securely in the system. Ameghino himself always regarded it as an insectivore allied to the African chrysochlorids. Scott (1905), in his description of excellent material collected by the Princeton Patagonian Expeditions, compared it with *Chrysochloris* and *Notoryctes* and concluded that it was an insectivore related to the African form: ''What does seem probable is that *Necrolestes* is an offshoot from some early member of the family which was at the same time the ancestor of *Chrysochloris.''* Gregory (1910, p. 259) and Schlosser and Woodward in various editions of Zittel accepted *Necrolestes* as an insectivore, but others have queried or denied such a relationship. Leche pointed out that *Necrolestes* resembled *Notoryctes* about as much as it did *Chrysochloris,* that as a marsupial it would raise fewer zoogeographical difficulties than as an insectivore, and that its affinities were far from decided: ''. . . die Beziehungen des Necrolestes zu den lebenden Säugern durch das bisher dargelegten material keineswegs als festgestellt betrachtet werden können'' (1907, p. 143). Abel (*in* Weber 1928, pp. 128-129), while discussing the genus under the Insectivora, expressed similar reservations. In current reference works, *Necrolestes* has been questionably included either among the marsupials (Romer 1945, p. 611) or among the insectivores (Simpson 1945, p. 53). Saban (1954, p. 422) has made the passing suggestion that it may be a palaeanodont edentate. One author who came out unequivocally for marsupial affinities was Winge (1941, pp. 79-80, 217-218), who regarded the incisor formula, reported by Scott to be $\frac{4}{4}$, as proof of such relationship. He believed *Necrolestes* to be a didelphoid derivative, classifying it in a separate division, Necrolestini, of his family Cladosictididae (=Borhyaenidae).

No first hand account of this little creature has appeared since Scott's study. His work was perforce done without benefit of the binocular microscope, and his conclusions as to affinities suffered from the fact that he evidently compared *Necrolestes* only with the equally highly specialized *Notoryctes* and the chrysochlorids, not at all with more generalized insectivores and marsupials. It had always seemed to me that a form represented by such excellent material — with most of the skeleton preserved in one or another of the Princeton specimens it is actually among the better known fossil mammals — should reveal enough in the way of structure to permit at least its infraclass affinities to be firmly established. Recent examination and further preparation of the Princeton material has shown this to be indeed the case. *Necrolestes* is beyond any doubt a marsupial and, as regards its position within the order, Winge's suggestion of a remote relationship with the borhyaenids is perhaps as reasonable a one as can now be offered. Scott's account is in general very good indeed. The brief description that follows is supplementary to his and corrects it in a few points.

I wish to express my sincere thanks to Professor Glenn L. Jepsen and to Dr. Donald F. Baird, who very kindly took the photographs from which the drawings prepared by Mrs. Dorothy Marsh were made.

MARSUPIALIA
BORHYAENOIDEA
NECROLESTIDAE

Necrolestes patagonensis Ameghino

Knowledge of the species, the only one of the family thus far discovered, rests essentially on three specimens in the Princeton collections:

15065. Skull, crushed dorsoventrally and lacking parts of occiput and basicranium, mandible (now missing), various vertebrae and ribs, proximal end of humerus. Ten miles South of Coy Inlet, Santa Cruz; collected by O. A. Peterson.

15384. Occiput and part of basicranium, mandible, some isolated upper teeth, numerous vertebrae from all parts of the column, pelvis, humerus, radius, ulna and various bones of the fore foot. Five miles South of Coy Inlet, Santa Cruz; collected by O. A. Peterson.

15699. Skull, incomplete posteriorly, mandible, right humerus, radius and ulna, left radius, incomplete ulna, femur, tibia, fibula, calcaneum, astragalus, cuboid. Killik Aike, Santa Cruz; collected by J. B. Hatcher.

DENTITION

Dental formula. It can be definitely stated that this is $I\frac{5}{4}$, $C\frac{1}{1}$, postcanines $\frac{6}{6}$ (probably $P\frac{2}{2}$, $M\frac{4}{4}$). Recognition of the correct number of upper incisors at this late date, more than half a century after the full account of the material, comes as somewhat of a surprise. The evidence is unmistakable, however (Fig. 1 A, B). In 15699, $I\frac{1\text{-}4}{}$ are preserved on the left side and the alveoli of these four teeth, together with $I\frac{5}{}$, on the right. No. 15065 retains right and left $I\frac{1}{}$, right $I\frac{5}{}$ and the alveoli of all other members of the series. Curiously enough, van Iterson, the artist who drew Scott's figures, indicated the correct number (Scott 1905, pl. 64, figs. 1, 2a). For 15699 he showed five incisors in right side view, reversing $I\frac{1\text{-}4}{}$ from the left side, and for 15065 the right and left $I\frac{1}{}$, right $I\frac{5}{}$ and the alveoli of right $I\frac{2\text{-}4}{}$ (the alveoli of left $I\frac{2\text{-}5}{}$ were at that time concealed by matrix). The figure of 15065 has right $I\frac{5}{}$ erroneously labeled as $I\frac{4}{}$. Determination of the postcanine formula is uncertain. Believing that he was dealing with an insectivore, Scott gave it as $P\frac{3}{3}$, $M\frac{3}{3}$. Since we have a marsupial on our hands, either this formula could be correct, with $M\frac{4}{4}$ missing, or the first premolar could be the missing tooth, which would give $P\frac{2}{2}$, $M\frac{4}{4}$. The latter possibility seems to me the more likely of the two. The last four cheek teeth above and below are uniform in structure, which suggests, although of course does not prove, that all are molars, while the second pair of teeth, especially the lower, although largely molariform, do show some resemblances to the anterior pair.

Upper teeth. The first four incisors are of similar structure, with the crowns rectangular, compressed anteroposteriorly, the labial face slightly convex in the dorsoventral diameter and bearing a faint median groove. I^{2} is the largest, I^{1} slightly smaller and $I^{3\text{-}4}$ of equal size and slightly smaller than I^{1}. I^{5} is the smallest of the series. It is a bluntly pointed tooth, worn obliquely on the posterior face by the anterior surface of the lower canine.

Relative to the sizes of the other teeth, the single-rooted, trihedral canines, both upper and lower, are enormous. The upper is somewhat variable, that of 15699 being stouter, more triangular and with a larger anterior face than that of 15065.

The first upper cheek tooth, P^{2} as here interpreted, is double-rooted, implanted obliquely, and consists of a high, conical paracone, an anterior basal cusp and a shearing edge running from the apex of the paracone to the large but non-cuspidate metastylar area. The remaining teeth of the postcanine series are unilaterally hypsodont, curving outward toward their bases and tapering to small, bluntly pointed single roots (Fig. 1C). The enamel extends nearly to the end of the root of the lingual surface and for only a short distance up the crown on the labial. $M^{1\text{-}3}$ are essentially narrow isosceles triangles as regards crown contour; P_{3} has a convex anterior and M^{4} a convex posterior border. $M^{1\text{-}2}$ are subequal, M^{3} is slightly smaller and M— reduced in size. The internal cusps are presumably paracones, being in line with the paracone of P^{2}, and the greater part of the crowns is formed by the stylar area. There is no vestige of a protocone. These teeth are thus descriptively zalambdodont, but no structural details are apparent in the worn material available.

Lower teeth. The incisors resemble those of the upper series and are not, as Scott stated, laterally compressed. I_{1} is much larger than the others, which are subequal. The canine is narrower and less trihedral than the upper, with a smaller anterior face.

P_{2} is double-rooted, elongate anteroposteriorly and bears three cusps, a high, acute protoconid and smaller, subequal anterior and posterior basal cusps. The molars are alike in structure and are mirror images of the uppers, with no traces of talonids. The second postcanine, P_{3} as I believe, differs from them in being less narrowly triangular and in the possession of a vestigial anterior basal cusp serially homologous with that occurring on $\mathrm{P}_{\overline{2}}$. The less worn of the lower molars available have heart-shaped crown contours caused by a shallow, ephemeral indentation between the bases of the paraconids and metaconids. No doubt $\mathrm{P}_{\overline{3}}$-$\mathrm{M}_{\overline{4}}$ are mirror images of the corresponding upper teeth as regards unilateral hypsodonty, enamel distribution and root structure but no loose examples are available. Wear on all molars is limited to the crowns, where the abrasion surfaces are nearly plane. It is quite evident that in active occlusion the trigonids of the lowers worked across the trigons of the uppers.

SKULL

As is the case in other small fossorial forms, no suture is apparent in any specimen of *Necrolestes.* The chief peculiarity of the skull is of course the extraordinary upturned snout, which extends well above and in front of the incisors (Fig. 1 A, B). Scott was in some doubt as to whether this feature might not have been exaggerated by distortion in 15699, particularly as there is little trace of it in 15065. It appears to be natural, however. No. 15699 has undergone slight lateral compression, in the course of which the maxillaries and premaxillaries have been broken away from and slightly pinched in relative to the nasals, but this does not appear to have affected the dorsal profile of the facial region. No. 15065 has been badly crushed dorsoventrally in this region and the upturned portion has been weathered off. The anterior narial openings (Fig. 1 A, B) extend forward to the tips of the nasals and do not end short of them, as Scott's figure shows them as doing. The median spine described by Scott as extending upward and forward from the mid-point of the premaxillaries evidently continued to the tips of the nasals as an ossification in the septum. It is partly broken away but remnants of it are still present. Between $\mathrm{I}^{\underline{3}}$ and the canines, the premaxillaries are very deeply excavated for the reception of the lower canines, perhaps the most extreme development of this character to be seen in the Marsupialia.

The upwardly arching zygomatic arch is well developed for so small an animal (Winge described it as slender, but this was in comparison with the arch of the borhyaenids) and quite similar to that of small didelphids such as *Marmosa*. Extension of the jugal to the glenoid articulation is a marsupial character. Despite the obliteration of the sutures, there can be little doubt that the jugal of *Necrolestes* was so constructed. A prominent preglenoid process is present. The glenoid surface extends forward to this buttress and is in consequence deeply concave anteroposteriorly. Precisely similar conditions exist in other marsupials, in which the buttress is formed by the jugal. A post-

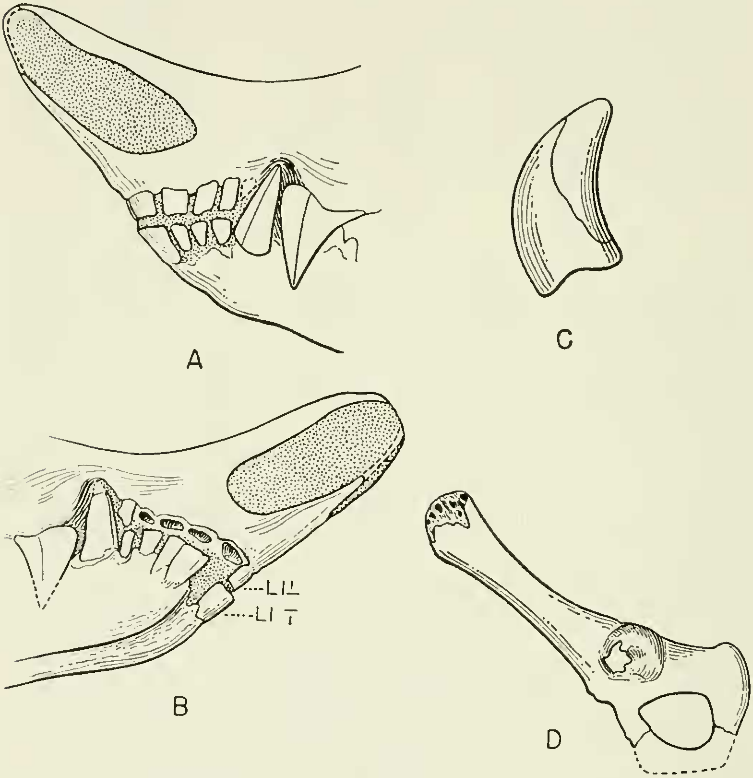

Fig. 1. *Necrolestes patagonensis* Ameghino. *A, B,* right and left sides of snout region of skull, X3 approx. (*LI,* left incisor); *C,* left M^2, anterior view, X6; *D,* left innominate bone, lateral view, X2 approx.

glenoid process is lacking. The extent of the lachrymal cannot, of course, be seen. The lachrymal foramen, however, is so very similar to that of various didelphids as regards both position and size (far more so than to that of the chrysochlorids, with which Scott compared it) as to suggest that the bone itself was likewise comparable. Within the orbito-temporal region, the optic foramen appears to be confluent with the sphenorbital fissure.

The long, slitlike incisive foramina are very didelphid-like, while the complete absence of palatal vacuities is a point of resemblance to the borhyaenids. The posterior border of the palate is moderately thickened and the posterior nares are divided by a median bony septum. For a marsupial this is very unusual; it may be an adaptation for providing an increased rigidity that would be useful to an animal using its upturned snout as an earth mover.

Specimens 15065 and 15384 reveal a good deal of the structure of the basicranium and auditory region, much of which had hitherto been concealed by matrix. The basicranium is very short. The greater part of the right side of the basisphenoid is preserved in 15065 and this portion is perforated, at the level of the glenoid cavity, by a large foramen, which appears to be the carotid. The bone is almost flat and there is no indication of a tympanic wing. The basioccipital, of which only a small part is preserved in 15384, was clearly short and wide. As noted by Scott, the condyles are relatively very large and wide; as in *Marmosa* there is a conspicuous median notch between them that opens forward from the foramen magnum. The latter opening is large and faces posteriorly. There is no paroccipital process, the ''broad and distinct'' process so identified by Scott being the mastoid. That part of the alisphenoid external to the foramen ovale, of which the lateral rim is preserved, is present in 15065; it shows no trace of any development of an alisphenoid bulla. It is perforated by a small foramen, presumably vascular, situated midway between the foramen ovale and the glenoid cavity. The periotic is short and robust, with a well rounded promontorium, which I take to have been the basis for Scott's incorrect statement that the ''tympanic bulla'' was ''ossified and moderately inflated.'' Anteriorly, the bone terminates bluntly and, posteriorly, there is no trace of a tympanic wing.

The fossa subarcuata is very large, and the anterior vertical semicircular canal is free from surrounding bone. The mastoid process appears to be large.

Immediately posterior to the glenoid cavity is a more or less triangular pocket, whose medial border is formed by the petrous portion of the periotic, the lateral by the squamosal and mastoid, which descend below the level of the glenoid and are concave on their medial surfaces, while the squamosal appears to be the main contributor to the roof, with the other elements participating to a lesser extent. A low transverse ridge crosses the roof of this pocket, partially dividing it into a large anterior portion, which is open below, and a smaller posterior portion, which is floored by the mastoid process. The fenestra ovalis and the apertura tympanici canalis facialis open into the pocket and the groove for the facial nerve is plainly visible in the lateral side of the periotic. This pocket, then, is the tympanic cavity, and the tympanic itself, of which no part remains, obviously provided a partial floor to the ventrally open anterior portion. There is no emargination of the squamosal marking the passage of the auditory meatus, which must have passed laterally below and behind the glenoid cavity. Within the pocket, in 15065, there is a minute foramen immediately behind the glenoid and a larger one just posterior to it. These I take to be the postzygomatic and postglenoid foramina. The tympanohyal, descending from the crista facialis, is fused with a small medial projection from the mastoid process in 15065 but stands free in 15384. The "foramen" stylomastoideum primitivum is entirely open, merely the termination of the facial groove, as in various didelphids. Posterior to the tympanohyal is the opening of a short tubular recess, covered laterally by the mastoid and exoccipital, that runs back to the condyle. An almost identical recess occurs in small didelphids, e.g. *Marmosa*, and presumably houses M. stapedius. Of the preserved foramina not heretofore mentioned, the lacerum posterius is large and the condylar, due to the shortness of the basicranium, is very close to it. The latter, so far as I can detect, is single. There appears to be no subsquamosal foramen.

The posterior portion of the mandible is greatly reduced and the angle consequently very small. Notwithstanding, this process bears an internal ledge and this is inflected and concave dorsally.

The fossorial specialization has resulted in a highly modified skeleton that shows numerous resemblances to other, similarly adapted forms, as Scott pointed out. Making due allowance for this, there is nothing that argues against a didelphoid ancestry for the Necrolestidae. The lack of an anticlinal vertebra, a point emphasized by Scott as a resemblance to the chrysochlorids is also true for the thoracic series of some of the smaller didelphids, and in these the neural spines of the lumbars do not incline forward to any appreciable extent. There is clear evidence of a well-developed tail, in agreement with didelphids and borhyaenids.

The proportions of the pelvis closely resemble those of the smaller didelphids and, as Scott pointed out, there was surely a well-developed pubic symphysis. The ilium is more rodlike than in the Didelphidae, a difference possibly related to the fossorial adaptation of *Necrolestes*. In very close agreement with didelphids, there is a conspicuous pectineal prominence that stands well out from the anterior margin of the pubis. The relatively large epipubis of the smaller opossums extends up nearly to the pectineal prominence, and I suspect that the same was true of *Necrolestes*. On the right side of 15384 there is a small fragment of bone attached to this area of the pelvis by matrix, and it is just conceivable that this could be a remnant of the epipubis itself.

DISCUSSION

Winge was correct in his opinion that *Necrolestes* was a marsupial. The incisor formula is diagnostic for a large segment of this order. There is nothing of a conflicting nature in the structure of the skull or postcranial skeleton; on the contrary numerous features described above point so strongly in the same direction that there is no further need to elaborate on the ordinal position of the genus. Saban was quite right in seeking to exclude the Necrolestidae from the Insectivora, and his tentative suggestion of palaeanodont affinities was a reasonable one, given the information in Scott's account. The new facts do not support it, however. The Palaeanodonta resemble the Xenarthra in the possession of an ossified bulla composed of ecto- and entotympanic elements (Patterson and Segall, MS.) which *Necrolestes* does not have; the dentition and the pelvis are quite different, and so on. There is, of course, a general resemblance between *Epoicotherium* and *Necrolestes* but, like the resemblance between the latter and the chrysochlorids, this is due to convergence.[1]

There remains for discussion the problem of where, within the Marsupialia, *Necrolestes* should be placed. The isolated position of the genus — its lack of any ancestors combined with its great specialization — prevents any satisfactory conclusion, although some approximation is possible. The facts of zoogeography would seem to limit the field to the known South American groups. One of these, the Caenolestoidea, may at once be excluded from consideration. No known caenolestoid approaches *Necrolestes* in any significant way; the dentitions of the earliest forms are specialized in completely different directions. The remaining two groups, the Didelphoidea and the Borhyaenoidea, on the contrary, do show resemblances of a basic sort to the Necrolestidae. Some of these have been mentioned in the description. As regards the dentition, the incisors of didelphids — and presumably of the earliest borhyaenids — could readily have given rise to those of *Necrolestes;* the canines are large in the two, and the lower is received into a socket in the upper jaw; the zalambdodont molar type of the necrolestids could readily have evolved from tribosphenic molars of the sort that were no doubt present in the early members of both groups. The skull and postcranial skeleton of *Necrolestes* reveal, beneath the façade of fossorial specialization, unmistakable borhyaenid and didelphid resemblances.

If, as seems virtually assured, the ancestry of the Necrolestidae is to be sought near the base of the didelphoid-borhyaenoid complex, then the question arises as to whether it is nearer to one or to the other of these superfamilies, or is equally distinct from both. *Necrolestes* is one of the most specialized of American marsupials, specialized in a manner totally unlike anything seen in the Didelphoidea or in the Borhyaenoidea. To seize upon this as an excuse for erecting a superfamily for the reception of one genus whose phylogeny is totally unknown, would be the height of irresponsibility, however. Furthermore, there are one or two characters that hint at a more acceptable possibility. As will be evident from the descriptive notes, there are more resemblances to the didelphids than to the borhyaenids in the anatomy of *Necrolestes.* This is not surprising: the didelphids include the least specialized of marsupials and no doubt retain a good deal of the ancestral structure relatively unmodified. The adequately known borhyaenids are relatively much more specialized and would therefore be less likely to display basic resemblances to *Necrolestes.* However, in such characters as the absence of palatal fenestrae and the lack of an alisphenoid bulla, *Necrolestes* is closer to all or some of the borhyaenids, which conceivably may indicate that the family arose from the borhyaenoid stock shortly after its divergence from the didelphoid. Such evidence, of course, is of the slenderest yet I nevertheless clutch at these straws and, in accord with Winge, very tentatively place the Necrolestidae in the Borhyaenoidea.[2] As a marsupial, *Necrolestes* adds one more example to the long series of convergences and parallelisms for which the extinct South American mammalian fauna is justly famous: one of convergence toward another order (Insectivora, Chrysochloridae), one of parallelism within the order (*Notoryctes*).

---

[1] Since this was written, McDowell (Bull. Amer. Mus. Nat. Hist., **115**, 173-4, 1958) has asserted that *Necrolestes* is a member of the suborder Xenarthra. In addition to the characters of the auditory region just cited that oppose reference to the suborder Palaeanodonta, the presence of rooted, enamel-covered teeth and the absence of the diagnostic xenarthran vertebral and pelvic structures prevent acceptance of this opinion.

With the removal of *Necrolestes* from the Insectivora, an order of mammals — one widespread elsewhere at an early date — has definitely been eliminated from the early Tertiary South American scene. As I have briefly stated (1957, p. 57), it is becoming evident that the earliest South American mammalian fauna must have been an unbalanced one, of the sort encountered on islands. If, as has usually been supposed in recent years, the Americas were united by land in the late Cretaceous and early Paleocene it is very difficult to understand the absence from the southern continent of any traces of multituberculates, insectivores, taeniodonts, creodonts, fissipeds and pantodonts, to name only the groups that are known, or may with confidence be inferred, to have been in existence in the north during all or part of this time.[3] That none of these would have made its way over a land connection had such then been in existence is improbable in the extreme. It appears to me much more likely that no such connection existed. Projecting backward in time from the known early Tertiary mammalian faunas of South America, it is possible to visualize the relatively few major groups represented as having evolved from a small number of successful colonizations by ancestors that survived the hazards of overseas transportation from North America by natural rafts. A minimum of three such colonizations would have sufficed, but a more plausible total would be four, perhaps even more. I am in full agreement with Darlington (1957, p. 364) on this point.

---

[2] I prefer Simpson's classification of the marsupials into six groups (1945) to those classifications that unite Didelphidae, Borhyaenidae and Dasyuridae into one. Admittedly, these families are closer to each other morphologically than any one of them is to other marsupial groups, but keeping them separate (or at least keeping the Australian and South American groups separate) accords better with the zoogeographical data, which, when adequately understood, have an importance for mammalian taxonomy and phylogeny that can hardly be overestimated.

One successful landfall by a breeding pair or by a gravid female could have started the marsupial radiation, and another the edentate. The various ungulate groups might conceivably have resulted from a single colonization, but at least two seems more probable. From small, generalized condylarths could have evolved the litopterns, astrapotheres, xenungulates and pyrotheres. The notoungulates, by far the largest and most varied group of South American hoofed mammals, were, I suspect, the descendants of ancestors that were already members of this order by the time they made their landfall; they may have arrived earlier than the condylarths. The really extraordinary abundance and diversity of notoungulates, especially notable by contrast with the other ungulate orders, would be at least partially explicable under this view. It is implied, of course, that the Notoungulata were of northern origin and that the known Holarctic forms — *Palaeostylops* of the late Paleocene of Mongolia and *Arctostylops* of the early Eocene of North America — were lingering survivors in that region. It is possible to think of these northern forms as immigrants from the south, but I am encouraged to doubt this by the structure of their teeth, which seems to me sufficiently different in detail from anything known among South American notoungulates as to indicate some independent evolution.

---

[3] Primates had almost surely come into existence by the early Paleocene. They make their first appearance in South America in the Colhuehuapian, which suggests that they may not have reached the continent until after the Mustersan, perhaps at about the same time as the rodents. With a group so rare in the fossil record there is always a large element of doubt as to the reality of absence, and I therefore omit them from the list, which is quite imposing enough without them.

From the haphazard, unbalanced beginning thus visualized, the South American mammalian fauna in time achieved balance of a sort peculiarly its own. The early immigrants had by chance drifted to an area whose size, physical diversity and multitude of available niches provided the space essential for such a development.

REFERENCES

Ameghino, F.

1891. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia austral — especies nuevas, adiciones y correciones. Rev. Argent. Hist. Nat., **1**: 289-328.

Darlington, P. J.

1957. Zoogeography: the geographical distribution of animals. New York: John Wiley and Sons, i-xiii, 1-675.

Gregory, W. K.

1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., **27**: 1-524.

Leche, W.

1907. Zur Entwicklungsgeschichte des Zahn-Systems der Saügetiere, zugleich ein Beitrag zur Stammesgeschichte dieser Tiergruppe. Zweite Teil: Phylogenie. Zweites Heft: Die Familien der Centetidae, Solenodontidae und Chrysochloridae. Zoologica, **20** (49): 1-158.

Patterson, B.

1957. Mammalian phylogeny. *In* Premier symposium sur la spécificité parasitaire des parasites des vertébrés. Neuchatel: Paul Attinger, 15-48.

Romer, A. S.

1945. Vertebrate paleontology. Chicago: The University of Chicago Press, i-ix, 1-687.

Saban, R.

1954. Phylogénie des insectivores. Bull. Mus. Nat. d'Hist. Nat. Paris, (2) **26**: 419-432.

SCOTT, W. B.

1905. Palaeontology. Part II. Insectivora. Repts. Princeton Univ. Expeds. Patagonia, **5:** 365-383.

SIMPSON, G. G.

1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., **85:** i-xvi, 1-350.

WEBER, M.

1928. Die Saügetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. Band II. Systematischer Teil. Jena: Gustav Fischer: i-xxiv, 1-898.

WINGE, H.

1941. The interrelationships of the mammalian genera. Volume 1. Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata. København: C. A. Reitzel: i-xii, 1-412.